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# Period-doubling bifurcation of a discrete metapopulation model with a delay in the dispersion terms[☆]

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**Abstract**

In this work the period-doubling bifurcation of a discrete metapopulation with delay in the dispersion terms is discussed. By using the central manifold method, the period-doubling bifurcation can be analyzed from the viewpoint of the dynamical system. Intensive simulation on this model shows the dynamics of the metapopulation is similar to that of a single logistic model as the bifurcation parameter $\mu$ increases when $0 \le b < 1/2$, where $b$ is the dispersion parameter.


*Keywords:* Metapopulation; Logistic; Dispersion; Period-doubling bifurcation; Fixed point; Periodic orbits; Stability

## 1. Introduction

Metapopulation is an important concept in several ecological fields, including population ecology, landscape ecology, and conservation biology, which provides a theoretical framework for studying spatially structured populations. There have been many studies on metapopulations using continuous time models; see [5–8]. But in the context of the discrete models, there are relatively few contributions in the literature. Recently, Gyllenberg et al. [3] considered a two-patch discrete time metapopulation model of coupled logistic difference equations and gave a characterization of the fixed point and 2-periodic orbits. Yakubu and Castillo-Chavez [9] studied a more general metapopulation model over $N$ patches. The effects of synchronous dispersal on discrete time metapopulation dynamics with local (patch) dynamics of the same (compensatory or overcompensatory) or mixed (compensatory and overcompensatory) types are explored in [9]. More recently, Huang and Zou [4] proposed the following model system:

$$\begin{cases} x(n+1) = \mu x(n)(1-x(n)) + d_2 y(n-k_2) - d_1 x(n-k_1), \\ y(n+1) = \nu y(n)(1-y(n)) + d_1 x(n-k_1) - d_2 y(n-k_2) \end{cases} \tag{1}$$

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where $d_1, d_2 \geq 0$ represent the dispersion rate, $0 < \mu, \nu < 4$ represent the growth rate, and $0 \leq x(n), y(n) < 1$ represent the population density of each subpopulation after $n$ generations. The model carries a delay in the dispersion terms to account for long distance dispersion. Only a special case of (1): $k_1 = k_2 = 1$ and $d_1 = d_2 = b$ (meaning symmetric dispersal) is considered, and the impact of the dispersion on the global dynamics of the metapopulation is obtained in [4]. It is very hard and challenging work to study system (1) directly either in theory or in simulation. In order to avoid the important biological features from being hidden behind the complexity caused by high dimensions and multiparameter, Zeng et al. in [10] just discuss Hopf bifurcation of a special case of (1): $k_1 = k_2 = 1$, $\nu = \mu$ and $d_1 = d_2 = b$, that is, the following model system:

$$\begin{cases} x(n+1) = \mu x(n)(1-x(n)) + b[y(n-1) - x(n-1)], \\ y(n+1) = \mu y(n)(1-y(n)) + b[x(n-1) - y(n-1)]. \end{cases} \tag{2}$$

In this work, we will deal with the period-doubling bifurcation of this model. Note that when $b = 0$, there is no coupling and each subpopulation in (2) is governed by a well known discrete logistic equation of the form

$$u(n+1) = \mu u(n)(1-u(n)). \tag{3}$$

This one-dimensional dynamical system has been studied extensively and its dynamics, such as the period-doubling process from a stable $2^{n-1}$-periodic orbit to a stable $2^n$-periodic orbit and a route to chaos as the parameter $\mu$ increases in [1], is well understood. Comparing our results for (2) with that for (3), we find that when $0 < b < 1/2$ the dynamics of (2) is similar to that of (3), but the period-doubling bifurcation cascade for (2) occurs earlier than that for the system (3). We can analytically prove that there exist period-doubling bifurcations at the positive fixed point and 2-periodic orbit of (2) when $0 \leq b < 1/2$. By simulation, we also make a conjecture that the system (2) undergoes a cascade of period-doubling bifurcation and finally becomes chaotic as $\mu$ increases if $0 \leq b < 1/2$. From the ecology viewpoint, when $\mu$ is increased, each subpopulation will oscillate in cycles of period $2^n$ (where $n$ increases from 1 to infinity), and finally vary randomly and boundedly.

The rest of this work is organized as follows. Section 2 reviews some known results on the model (2). Section 3 is devoted to our main results. By using a change of coordinates and the central manifold method, the first period-doubling bifurcation and the second period-doubling bifurcation of (2) are analyzed in Section 3. Finally, some discussions and conjectures are given in Section 4.

## 2. Preliminaries

In this section, we first review some results about the model (2); for details, see [4,10]. We only consider the nonnegative solutions of (2) from the viewpoint of ecology, i.e. $x(n), y(n) \geq 0$ for any integer $n$. When $b = 0$, the dynamics of (2) is determined by the one-dimensional logistic equation (3). It is well known that the logistic equation undergoes a period-doubling cascade as $\mu$ increases, that is, there exists a sequence $\mu_0 = 1 < \mu_1 = 3 < \mu_2 = 1 + \sqrt{6} < \mu_3 < \cdots < \mu_n < \cdots < \mu_\infty \approx 3.56994$ such that when $\mu \in (\mu_n, \mu_{n+1})$, $n = 0, 1, 2, \ldots$, (3) has a unique stable $2^n$-periodic orbit.

For $\mu \in (\mu_n, \mu_{n+1})$, let $\{u_i, i = 1, 2, \ldots, 2^n\}$ be the corresponding stable $2^n$-periodic orbit of the logistic equation (3). Then $\{(u_i, u_i), i = 1, 2, \ldots, 2^n\}$ is a $2^n$-periodic orbit of (2) for any $b > 0$. Letting

$$w_1(n) = \frac{x(n) + y(n)}{2}, \qquad w_2(n) = \frac{x(n-1) - y(n-1)}{2}, \qquad w_3(n) = \frac{x(n) - y(n)}{2},$$

we can rewrite the difference system (2) as the three-dimensional discrete dynamical system

$$\begin{pmatrix} w_1(n+1) \\ w_2(n+1) \\ w_3(n+1) \end{pmatrix} = \begin{pmatrix} \mu(w_1(n) - w_1(n)^2 - w_3(n)^2) \\ w_3(n) \\ \mu(w_3(n) - 2w_1(n)w_3(n)) - 2bw_2(n) \end{pmatrix} \triangleq G \begin{pmatrix} w_1(n) \\ w_2(n) \\ w_3(n) \end{pmatrix}. \tag{4}$$

Since the dynamics of the system (2) is qualitatively the same as that of the system (4), we only need to analyze the system (4) qualitatively. By the above transformation, the $2^n$-periodic orbit $\{(u_i, u_i), i = 1, 2, \ldots, 2^n\}$ of the system (2) is transformed to the $2^n$-periodic orbit $\{W_{2^n}^i, i = 1, 2, \ldots, 2^n\}$ of the system (4), where $W_{2^n}^i = (u_i, 0, 0)^T$. By a simple computation, one can obtain the positive fixed point $W_1^1 = (1 - \frac{1}{\mu}, 0, 0)^T$, $\mu > \mu_0$ and the 2-periodic orbit $\{W_2^i = (u_i, 0, 0)^T, i = 1, 2\}$, $\mu > \mu_1$, where

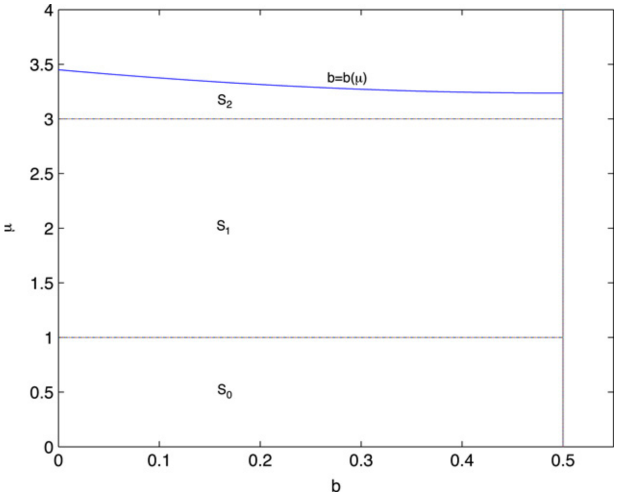


Fig. 1. The stability regions $S_0$, $S_1$, $S_2$ of $W^0$, $W_1^1$, $W_2^i$ $(i = 1, 2)$.

$$u_{1,2} = \frac{(\mu + 1) \pm \sqrt{(\mu + 1)(\mu - 3)}}{2\mu}.$$

From [4,10], we introduce the following lemmas concerning the qualitative results for $W^0 = (0, 0, 0)^T$, $W_1^1$ and $\{W_2^i, i = 1, 2\}$.

**Lemma 1.** (i) *If $1 < \mu \le 4$ and $b > 1/2$, then every period $p = 2^n$ orbit $W_{2^n}^i = (u_i, 0, 0)^T$ of (4), $i = 1, 2, \ldots, p$, is unstable.*

(ii) *If $\mu_0 = 1 < \mu < 3 = \mu_1$ and $0 \le b < 1/2$, then the positive fixed point $W_1^1 = (1 - \frac{1}{\mu}, 0, 0)^T$ of (4) is stable.*

(iii) *If $3 < \mu \le 1 + \sqrt{5}$ and $0 \le b < 1/2$ or $1 + \sqrt{5} < \mu < 1 + \sqrt{6}$ and $0 \le b < b(\mu)$, then the 2-periodic orbit $\{W_2^i = (u_i, 0, 0)^T, i = 1, 2\}$ is stable, where*

$$b(\mu) \triangleq \frac{1 - \sqrt{\mu^2 - 2\mu - 4}}{2} \in \left(0, \frac{1}{2}\right).$$

**Lemma 2.** (i) *If $0 < \mu < 1$ and $b > \frac{\mu^2}{8}$, then the system (4) undergoes a supercritical Hopf bifurcation at $(W, b) = ((W^0)^T, 1/2)$, and hence an attracting invariant closed curve exists, surrounding $W^0$ for $b > 1/2$ and $|b - 1/2|$ small.*

(ii) *If $1 < \mu < 3$ and $b > \frac{(2-\mu)^2}{8}$, then the system (4) undergoes a supercritical Hopf bifurcation at $(W, b) = ((W_1^1)^T, 1/2)$.*

(iii) *If $3 < \mu < 1 + \sqrt{5}$ and $b > \frac{(\mu-1)^2-5}{-8}$, then the system (4) undergoes a supercritical Hopf bifurcation at every 2-periodic orbit $(W, b) = ((W_2^i)^T, 1/2)$, $i = 1, 2$.*

From Lemma 1, the stable parameter regions $S_0$, $S_1$, $S_2$ of $W^0$, $W_1^1$, $W_2^i$ $(i = 1, 2)$ are depicted in Fig. 1. In [10], we made the conjecture that there exists Hopf bifurcation and period-doubling bifurcation in the discrete metapopulation model (2) in a different parameter region, and Hopf bifurcation of the system (4) (or the system (2)) has been proved by using the central manifold method. From now on, we begin to discuss the period-doubling bifurcation cascade of the system (4) under the condition $0 \le b < 1/2$.

## 3. The first and the second period-doubling bifurcations

Firstly, we consider the first period-doubling bifurcation of the system (4). Before giving our results, it is necessary to introduce the following lemma concerning period-doubling bifurcation (or flip bifurcation) in [2].

**Lemma 3.** *Let $f_\mu(x)$: $\mathbb{R} \to \mathbb{R}$ be a one-parameter family of mappings such that $f_{\mu_0}$ has a fixed point $x_0$ with eigenvalue $-1$. Assume*

(F1) $\dfrac{\partial f}{\partial \mu}\dfrac{\partial^2 f}{\partial x^2} + 2\dfrac{\partial^2 f}{\partial x \partial \mu} \neq 0$ *at* $(x_0, \mu_0)$;

(F2) $a = \dfrac{1}{2}\left(\dfrac{\partial^2 f}{\partial x^2}\right)^2 + \dfrac{1}{3}\left(\dfrac{\partial^3 f}{\partial x^3}\right) \neq 0$ *at* $(x_0, \mu_0)$.

*Then there is a smooth curve of fixed points of $f_\mu$ passing through $(x_0, \mu_0)$, the stability of which changes at $(x_0, \mu_0)$. There is also a smooth curve $\gamma$ passing through $(x_0, \mu_0)$ so that $\gamma - \{(x_0, \mu_0)\}$ is a union of hyperbolic period 2 orbits. The curve $\gamma$ has quadratic tangency with the line $\mathbb{R} \times \{\mu_0\}$ at $(x_0, \mu_0)$. And if $a$ is positive, the period 2 orbits are stable; if $a$ is negative, they are unstable.*

Next, by using the central manifold method and the period-doubling bifurcation lemma stated above, we obtain the following theorems.

**Theorem 1.** *If $0 \le b < 1/2$, then the system (4) undergoes a supercritical flip bifurcation at $(W, \mu) = ((W_1^1)^T, 3)$, i.e. the period 2 orbits bifurcating from $((W_1^1)^T, 3)$ are stable.*

**Proof.** Simple computation shows that one of the eigenvalues of Jacobian $DG(W, \mu)$ at $(W, \mu) = ((W_1^1)^T, 3)$ in (4) is $2 - \mu = -1$, the other two eigenvalues having modulus less than 1. So we can use central manifold theorem to reduce the dimension of the system (4). To this end, we first need to make a change of coordinates. Let

$$r_1 = w_1 - \left(1 - \frac{1}{\mu}\right), \qquad r_2 = w_2, \qquad r_3 = w_3, \qquad \tilde{\mu} = \mu - 3.$$

Then the system (4) can be written as the following system:

$$\begin{cases} r_1(n+1) = -r_1(n) - \tilde{\mu} r_1(n) - 3r_1(n)^2 - 3r_3(n)^2 - \tilde{\mu} r_1(n)^2 - \tilde{\mu} r_3(n)^2 \\ r_2(n+1) = r_3(n) \\ r_3(n+1) = -2br_2(n) - r_3(n) - \tilde{\mu} r_3(n) - 6r_1(n)r_3(n) - 2\tilde{\mu} r_1(n) r_3(n) \\ \tilde{\mu}(n+1) = \tilde{\mu}(n) = \tilde{\mu}. \end{cases} \tag{5}$$

By direct computation, we know that the fixed point $W_1^1$ of the system (4) is transformed to the fixed point $R^1 = (r_1, r_2, r_3) = (0, 0, 0)$ of the system (5). From the central manifold theorem in [2], it is known that for the system (5) central manifolds passing through $(R, \tilde{\mu}) = (R^1, 0)$ exist. Now we seek central manifolds as a graph

$$r_2 = d_2 r_1^2 + e_2 r_1 \tilde{\mu} + f_2 \tilde{\mu}^2 + g_2 r_1^3 + h_2 r_1^2 \tilde{\mu} + j_2 r_1 \tilde{\mu}^2 + k_2 \tilde{\mu}^3 + O(4),$$
$$r_3 = d_3 r_1^2 + e_3 r_1 \tilde{\mu} + f_3 \tilde{\mu}^2 + g_3 r_1^3 + h_3 r_1^2 \tilde{\mu} + j_3 r_1 \tilde{\mu}^2 + k_3 \tilde{\mu}^3 + O(4),$$

where $O(4)$ means the higher order terms about $r_1, \tilde{\mu}$ whose orders are not less than 4. Substituting the above expressions of central manifolds into (5), it is obtained that $d_i = e_i = f_i = g_i = h_i = j_i = k_i = 0, i = 1, 2$. So we can derive the reduction equation of the system (5) as follows:

$$r_1(n+1) = -r_1(n) - \tilde{\mu} r_1(n) - 3r_1(n)^2 - \tilde{\mu} r_1(n)^2 + O(4) \triangleq f(r_1(n), \tilde{\mu}). \tag{6}$$

After simple computation, one can prove that the conditions of the Lemma 3 hold, that is,

$$\left.\frac{\partial f}{\partial r_1}\right|_{(r_1,\tilde{\mu})=(0,0)} = -1, \qquad \left.\left(\frac{\partial f}{\partial \tilde{\mu}}\frac{\partial^2 f}{\partial r_1^2} + 2\,\frac{\partial^2 f}{\partial r_1 \partial \tilde{\mu}}\right)\right|_{(0,0)} = -2 \neq 0,$$

$$a = \left.\left(\frac{1}{2}\left(\frac{\partial^2 f}{\partial r_1^2}\right)^2 + \frac{1}{3}\left(\frac{\partial^3 f}{\partial r_1^3}\right)\right)\right|_{(r_1,\tilde{\mu})=(0,0)} = 18 > 0.$$

Therefore the reduction system (6) undergoes a supercritical flip bifurcation at $(r_1, \tilde{\mu}) = (0, 0)$, and hence the system (4) undergoes a supercritical flip bifurcation at $(W, \mu) = ((W_1^1)^T, 3)$. The conclusion holds. $\square$

Next, we will consider the second period-doubling bifurcation of the system (4) for the 2-periodic orbit $W_2^i = (u_i, 0, 0)^T$, $i = 1, 2$, where

$$u_{1,2} = \frac{(\mu+1) \pm \sqrt{(\mu+1)(\mu-3)}}{2\mu}.$$

Note that when $0 \le b < 1/2$, $\mu > 3$, the separatrix of the stable region and the unstable region of the above 2-periodic orbit is depicted by the curve

$$b = b(\mu) \triangleq \frac{1 - \sqrt{\mu^2 - 2\mu - 4}}{2} \in \left(0, \frac{1}{2}\right),$$

or

$$\mu = \mu(b) \triangleq 1 + \sqrt{4b^2 - 4b + 6} \in (1 + \sqrt{5}, 1 + \sqrt{6}).$$

By using the same method as above, we can derive the theorem below, but we need more patience to deal with the complicated proof.

**Theorem 2.** *If $0 \le b < 1/2, \mu > 3$, then for any point $(b, \mu) = (\bar{b}, \bar{\mu})$ on the curve $b = b(\mu)$, the second composition $G^2$ of $G$ undergoes a supercritical flip bifurcation at $(W, \mu) = ((W_2^i)^T, \bar{\mu})$ $(i = 1, 2)$ when $b = \bar{b}$ is fixed and $\mu$ varies near $\bar{\mu}$, that is, the system (4) undergoes the second supercritical flip bifurcation when the parameter pair $(b, \mu)$ crosses the curve $b = b(\mu)$.*

**Proof.** When $b = 0$, the system (4) (or the system (2)) is determined by the logistic equation (3); the conclusions of Theorem 2 hold obviously. Next we consider the case $0 < b < 1/2$.

Step 1: Compute the second composition $G^2$ of $G$, i.e.

$$\begin{pmatrix} w_1(n+2) \\ w_2(n+2) \\ w_3(n+2) \end{pmatrix} = G^2 \begin{pmatrix} w_1(n) \\ w_2(n) \\ w_3(n) \end{pmatrix} = \begin{pmatrix} G_1(w_1(n), w_2(n), w_3(n)) \\ G_2(w_1(n), w_2(n), w_3(n)) \\ G_3(w_1(n), w_2(n), w_3(n)) \end{pmatrix}, \tag{7}$$

where

$$\begin{aligned} G_1(w_1, w_2, w_3) &= \mu^2 w_1 - (\mu^2 + \mu^3) w_1^2 - (\mu^2 + \mu^3) w_3^2 - 4b^2 \mu w_2^2 + 4b\mu^2 w_2 w_3 + 2\mu^3 w_1^3 \\ &\quad + 6\mu^3 w_1 w_3^2 - 8b\mu^2 w_1 w_2 w_3 - \mu^3 w_1^4 - 6\mu^3 w_1^2 w_3^2 - \mu^3 w_3^4, \\ G_2(w_1, w_2, w_3) &= -2b w_2 + \mu w_3 - 2\mu w_1 w_3, \\ G_3(w_1, w_2, w_3) &= -2b\mu w_2 + (\mu^2 - 2b) w_3 - 2(\mu^2 + \mu^3) w_1 w_3 + 4b\mu^2 w_1 w_2 - 4b\mu^2 w_1^2 w_2 \\ &\quad - 4b\mu^2 w_2 w_3^2 + 6\mu^3 w_1^2 w_3 + 2\mu^3 w_3^3 - 4\mu^3 w_1^3 w_3 - 4\mu^3 w_1 w_3^3. \end{aligned}$$

In order to discuss the flip bifurcation for the 2-periodic orbit $W_2^i$, $i = 1, 2$, we only need to analyze the discrete dynamics system (7) determined by the mapping $G^2$ for $W_2^1$; the discussion about $W_2^2$ is entirely similar.

Step 2: Change of coordinates

For any $b = \bar{b}$ fixed, $\mu$ varies near $\bar{\mu}$. Here $\bar{\mu} = 1 + \sqrt{4b^2 - 4b + 6}$, and we define $\bar{q} = \sqrt{\bar{\mu}^2 - 2\bar{\mu} - 3}$. Let

$$\begin{cases} v_1 = w_1 - u_1 \\ v_2 = \dfrac{2b}{1+2b} w_2 - \dfrac{\bar{q} - 1}{1 - 4b^2} w_3 \\ v_3 = \dfrac{1}{1+2b} w_2 + \dfrac{\bar{q} - 1}{1 - 4b^2} w_3 \\ \tilde{\mu} = \mu - \bar{\mu} \end{cases}$$

where

$$u_1 = \frac{(\mu+1) - \sqrt{(\mu+1)(\mu-3)}}{2\mu}.$$

By the change of coordinates and Taylor expansion, we obtain the following equivalent system for (7):

$$\begin{pmatrix} v_1(n+2) \\ v_2(n+2) \\ v_3(n+2) \\ \tilde{\mu}(n+2) \end{pmatrix} = H \begin{pmatrix} v_1(n) \\ v_2(n) \\ v_3(n) \\ \tilde{\mu}(n) \end{pmatrix} = \begin{pmatrix} H_1(v_1(n), v_2(n), v_3(n), \tilde{\mu}(n)) \\ H_2(v_1(n), v_2(n), v_3(n), \tilde{\mu}(n)) \\ H_3(v_1(n), v_2(n), v_3(n), \tilde{\mu}(n)) \\ H_4(v_1(n), v_2(n), v_3(n), \tilde{\mu}(n)) \end{pmatrix} \tag{8}$$

where

$$\begin{aligned}
H_1(v_1, v_2, v_3, \tilde{\mu}) &= [-\tilde{\mu}^2 + 2(1-\bar{\mu})\tilde{\mu} + 1 - \bar{q}^2]v_1 + \left[P\tilde{\mu} + \bar{\mu}(3\bar{q} - \bar{q}^2)\right] v_1^2 + \left[\left(\frac{4b + \bar{q} - 1}{\bar{q}(\bar{q}-1)}\bar{\mu}(\bar{\mu}-1)\right.\right. \\
&\quad + \left.\frac{\bar{q}^2 + \bar{q} + 2}{\bar{q} - 1}\right)\tilde{\mu} + \left.\frac{\bar{q}^2 + \bar{q} + 2}{\bar{q} - 1}\bar{\mu}\right] v_2^2 + \left[\left(-16b^3 + 8b^2 - 4b - \frac{4b(2b-1)^2\bar{\mu}(\bar{\mu}-1)}{\bar{q}(\bar{q}-1)}\right.\right. \\
&\quad - \left.\frac{4b(2b-1)^2}{(\bar{q}-1)^2}P\right)\tilde{\mu} + \left.\left(\bar{\mu}(-16b^3 + 8b^2 - 4b) - \frac{4b(2b-1)^2}{(\bar{q}-1)^2}(3\bar{q} - \bar{q}^2)\bar{\mu}\right)\right] v_2 v_3 \\
&\quad + \left[\left(4b^2 - 16b^3 + \frac{(8b^2 - 16b^3)\bar{\mu}(\bar{\mu}-1)}{\bar{q}(\bar{q}-1)} + \frac{(2b - 4b^2)^2}{(\bar{q}-1)^2}P\right)\tilde{\mu} + \left(\bar{\mu}(4b^2 - 16b^3)\right.\right. \\
&\quad + \left.\left.\frac{(2b - 4b^2)^2(3\bar{q} - \bar{q}^2)\bar{\mu}}{(\bar{q}-1)^2}\right)\right] v_3^2 + 2(\bar{q}-1)\bar{\mu}^2 v_1^3 + \frac{2\bar{\mu}^2(2b-1)(2b-3)}{\bar{q}-1}v_1 v_2^2 \\
&\quad + \frac{8\bar{\mu}^2 b^2(1-2b)(1-6b)}{\bar{q}-1}v_1 v_3^2 - \frac{16b(2b-1)^2\bar{\mu}^2}{\bar{q}-1}v_1 v_2 v_3 + O(4), \\
H_2(v_1, v_2, v_3, \tilde{\mu}) &= \left(-1 + \frac{2(1-\bar{\mu})}{1-4b^2}\tilde{\mu} + \frac{8b^3 - 12b^2 + 16b - 2}{(1-4b^2)\bar{q}^2}\tilde{\mu}^2\right) v_2 + \left[\left(\frac{-2b\bar{q}}{1+2b} + \frac{2b}{1-2b}\right)\right. \\
&\quad \cdot \left(\frac{\bar{\mu}-1}{\bar{q}} - \frac{2}{\bar{q}^3}\tilde{\mu}\right) + \frac{4b(\bar{\mu}-1)}{1+2b} + \left.\frac{2b}{1+2b}\tilde{\mu}\right]\tilde{\mu} v_3 + \left[\left(\frac{4b(1-2b)}{(2b+1)(\bar{q}-1)}\right.\right. \\
&\quad + \left.\frac{2}{1+2b}P - \frac{4b(\bar{q}-1)}{1-4b^2}(\bar{q} - 1 + \bar{\mu}(\bar{\mu}-1)/\bar{q})\right)\tilde{\mu} + \left.\frac{2(3\bar{q} - \bar{q}^2)\bar{\mu}}{1-4b^2}\right] v_1 v_2 \\
&\quad + \left[\left(\frac{-8b^2(1-2b)}{(1+2b)(\bar{q}-1)} - \frac{4b}{1+2b}P - \frac{4b(\bar{q}-1)}{1-4b^2}(\bar{q} - 1 + \bar{\mu}(\bar{\mu}-1)/\bar{q})\right)\tilde{\mu}\right. \\
&\quad + \left.\frac{\bar{\mu}}{1-4b^2}\left(-8b^2\bar{q}^2 + (16b^2 - 4b)\bar{q} - 8b^2 - 4b\right)\right] v_1 v_3 \\
&\quad + \frac{(6-8b)(\bar{q}-1)\bar{\mu}^2}{1-4b^2}v_1^2 v_2 + \frac{24b^2 - 8b}{1-4b^2}(\bar{q}-1)\bar{\mu}^2 v_1^2 v_3 \\
&\quad + \frac{(2-4b)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}v_2^3 + \frac{8b(1-b)(2b-1)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}v_2^2 v_3 \\
&\quad + \frac{8b^2(1-2b)(1-4b)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}v_2 v_3^2 + \frac{32b^4(1-2b)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}v_3^3 + O(4), \\
H_3(v_1, v_2, v_3, \tilde{\mu}) &= \left[\left(-\frac{\bar{q}}{1+2b} - \frac{1}{1-2b}\right)\left(\frac{\bar{\mu}-1}{\bar{q}} - \frac{2}{\bar{q}^3}\tilde{\mu}\right)\tilde{\mu} + \frac{2(\bar{\mu}-1)}{1+2b} + \frac{1}{1+2b}\tilde{\mu}\right]\tilde{\mu} v_2 \\
&\quad + \left(-4b^2 + \frac{8b^2(\bar{\mu}-1)}{1-4b^2}\tilde{\mu} + \frac{16b^4 - 24b^3 + 16b^2 - 12b}{(1-4b^2)\bar{q}^2}\tilde{\mu}^2\right) v_3 \\
&\quad + \left[\left(\frac{2-4b}{(1+2b)(\bar{q}-1)} - \frac{2}{1+2b}P + \frac{4b(\bar{q}-1)}{1-4b^2}\left(\bar{q} - 1 + \frac{\bar{\mu}(\bar{\mu}-1)}{\bar{q}}\right)\right)\tilde{\mu}\right. \\
&\quad + \left.\frac{2\bar{\mu}}{1-4b^2}\left(\bar{q}^2 + (2b-2)\bar{q} + 2b + 1\right)\right] v_1 v_2 \\
&\quad + \left[\left(\frac{8b^2(\bar{q}^2 - 3\bar{q})}{1-4b^2} + \frac{4b\bar{\mu}(\bar{\mu}-1)}{(1-4b^2)\bar{q}}(2 - 6b + (4b-1)\bar{q})\right)\tilde{\mu} + \frac{8b^2\bar{\mu}\bar{q}(\bar{q}-3)}{1-4b^2}\right] v_1 v_3 \\
&\quad + \frac{(8b-6)(\bar{q}-1)\bar{\mu}^2}{1-4b^2}v_1^2 v_2 + \frac{(8b - 24b^2)(\bar{q}-1)\bar{\mu}^2}{1-4b^2}v_1^2 v_3 + \frac{(4b-2)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}v_2^3 \\
&\quad + \frac{8b(1-2b)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}\left[(1-b)v_2^2 v_3 - b(1-4b)v_2 v_3^2 - 4b^3 v_3^3\right] + O(4),
\end{aligned}$$

$$H_4(v_1, v_2, v_3, \tilde{\mu}(n)) = \tilde{\mu}(n) = \tilde{\mu} \quad \text{for any integer } n \geq 0.$$

Here

$$P = \bar{\mu}(\bar{\mu}-1)\left(\frac{3}{\bar{q}} - 2\right) + 3\bar{q} - \bar{q}^2, \quad \tilde{\mu} < \bar{\mu} - 3,$$

where $O(4)$ denotes the higher order terms about $v_1, v_2, v_3, \tilde{\mu}$ whose orders are not less than 4.

Step 3: Dimension reduction

By computation, one knows that the eigenvalues $\lambda_i (i = 1, 2, 3, 4)$ of $DH(v_1, v_2, v_3, \tilde{\mu})$ at $(v_1, v_2, v_3, \tilde{\mu}) = (0, 0, 0, 0)$ satisfy $-1 < \lambda_1 = 1 - \bar{q}^2 < 0$, $\lambda_2 = -1$, $-1 < \lambda_3 = -4b^2 < 0$, $\lambda_4 = 1$. So, we use the central manifold theorem to obtain central manifolds as a graph

$$v_1 = A_1 v_2^2 + E_1 v_2^2 \tilde{\mu} + (\text{higher order terms}), \qquad v_3 = B_3 v_2 \tilde{\mu} + D_3 v_2^3 + F_3 v_2 \tilde{\mu}^2 + (\text{higher order terms}),$$

where

$$\begin{aligned}
A_1 &= \frac{(\bar{q}^2 + \bar{q} + 2)\bar{\mu}}{\bar{q}^2(\bar{q}-1)}, \\
B_3 &= \frac{-(1-2b)\bar{q} + 1 + 2b}{(1-4b^2)^2} \cdot \frac{\bar{\mu}-1}{\bar{q}}, \\
D_3 &= \frac{1}{4b^2-1}\left[\frac{2\bar{\mu}}{1-4b^2}\left(\bar{q}^2 + (2b-2)\bar{q} + 2b + 1\right) A_1 + \frac{(4b-2)\bar{\mu}^2}{(1+2b)(\bar{q}-1)}\right], \\
F_3 &= \frac{1}{4b^2-1}\left[\frac{1}{1+2b} + \frac{2}{\bar{q}^3}\left(\frac{\bar{q}}{1+2b} + \frac{1}{1-2b}\right) - \frac{1-\bar{\mu}}{1-4b^2}(8b^2+2)B_3\right], \\
E_1 &= \frac{1}{\bar{q}^2}\left\{\frac{(1-\bar{\mu})(-8b^2+6)}{1-4b^2} A_1 + \frac{\bar{q}^2 + \bar{q} + 2}{\bar{q}-1} + \frac{4b + \bar{q} - 1}{\bar{q}(\bar{q}-1)}\bar{\mu}(\bar{\mu}-1) - \left[8b^2 + \frac{4b(\bar{q}+1)^2}{\bar{q}-1}\right]\bar{\mu} B_3\right\}.
\end{aligned}$$

Substituting the above expressions for central manifolds into the system (8), there follows the reduction equation of the system (8), that is,

$$\begin{aligned}
v_2(n+2) &= -v_2(n) + \frac{2(1-\bar{\mu})}{1-4b^2}\tilde{\mu} v_2(n) \\
&\quad + \left[\frac{8b^3 - 12b^2 + 16b - 2}{(1-4b^2)\bar{q}^2} + \frac{(\bar{\mu}-1)}{\bar{q}}\left(\frac{2b\bar{q}}{1+2b} + \frac{2b}{1-2b}\right) B_3\right]\tilde{\mu}^2 v_2(n) \\
&\quad + \frac{4(\bar{q}^2+3)\bar{\mu}^2}{(1-4b^2)\bar{q}(\bar{q}-1)} v_2(n)^3 + (\text{higher order terms}) \triangleq f(v_2(n), \tilde{\mu}).
\end{aligned} \tag{9}$$

By computation, we have

$$\left.\frac{\partial f}{\partial v_2}\right|_{(v_2,\tilde{\mu})=(0,0)} = -1, \quad \left.\left(\frac{\partial f}{\partial \tilde{\mu}}\frac{\partial^2 f}{\partial v_2^2} + 2\frac{\partial^2 f}{\partial v_2 \partial \tilde{\mu}}\right)\right|_{(0,0)} = \frac{4(1-\bar{\mu})}{1-4b^2} \neq 0,$$

$$a = \left.\left(\frac{1}{2}\left(\frac{\partial^2 f}{\partial v_2^2}\right)^2 + \frac{1}{3}\left(\frac{\partial^3 f}{\partial v_2^3}\right)\right)\right|_{(v_2,\tilde{\mu})=(0,0)} = \frac{8(\bar{q}^2+3)\bar{\mu}^2}{(1-4b^2)\bar{q}(\bar{q}-1)} > 0.$$

So the conditions of Lemma 3 hold; then the reduction system (9) undergoes a supercritical flip bifurcation at $(v_2, \tilde{\mu}) = (0, 0)$. Hence, the system decided by $G^2$ undergoes a supercritical flip bifurcation at $(W, \mu) = ((W_2^i)^T, \bar{\mu})$ $(i = 1, 2)$, the stable 4-periodic orbit of (4) begins to appear if $\mu > \bar{\mu}$. Because of the arbitrariness of $b$, the system (4) undergoes a second supercritical flip bifurcation when the parameter pair $(b, \mu)$ crosses the curve $b = b(\mu)$. □

**Remark 1.** From the results obtained above and in [4], when $b = \bar{b}(0 < b < 1/2)$ is fixed and $\mu$ is varied, we obtain:

(i) $0 < \mu < 1$: the metapopulation becomes globally extinct.
(ii) $\mu = 1$: $W^0$ and $W_1^1$ exchange stability in a transcritical bifurcation.

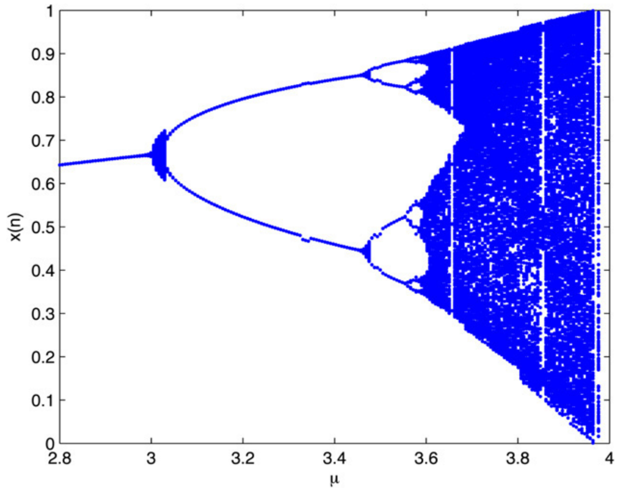


Fig. 2. The bifurcation diagram of $x(n)$ for the system (2) at $b = 0.01$.

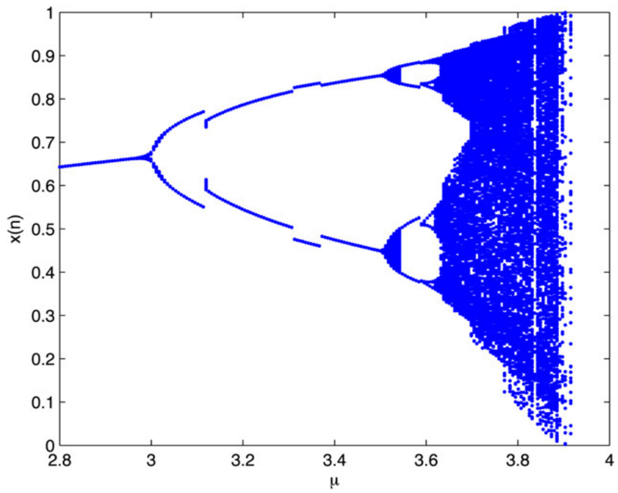


Fig. 3. The bifurcation diagram of $x(n)$ for the system (2) at $b = 0.03$.

(iii) $1 < \mu < 3$: the system settles down at a fixed point where both subpopulations are fixed in time.
(iv) $\mu = 3$: the first period-doubling bifurcation takes place.
(v) $3 < \mu < \bar{\mu}(\triangleq 1 + \sqrt{4b^2 - 4b + 6})$: the stable 2-periodic orbit of the system (2) begin to appear, and each subpopulation oscillates in a 2-periodic orbit.
(vi) $\mu = \bar{\mu}$: the second period-doubling bifurcation takes place; the stable 4-periodic orbit begins to appear if $\mu > \bar{\mu}$ and each subpopulation oscillates in a 4-periodic orbit.

## 4. Conclusions

In this work, the first and the second supercritical flip bifurcations of a discrete metapopulation model are proved by using the central manifold method. From the bifurcation diagrams of the system (2) in Figs. 2–4, it can be seen that our results fit well with the simulation, and we should be able to make a conjecture that the original system (2) may undergo a period-doubling cascade, and this can even result in a route to chaos if $0 < b < 1/2$. But it is a pity that we do not prove the existence of chaos in the system (2) from mathematical theory and only verify the conjecture by simulation; see Figs. 2–4. Comparing Fig. 2 with Fig. 3 and Fig. 4, we also find that the bigger $b$ becomes, the easier it becomes for the periodic orbits to lose stability and chaos to arise; and some solutions will approach infinity at the end

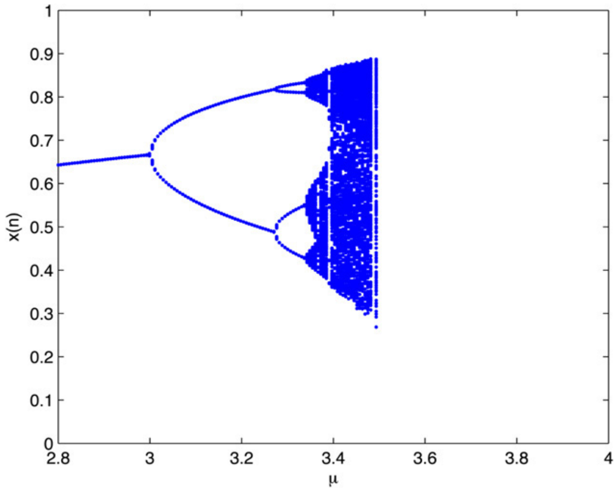


Fig. 4. The bifurcation diagram of $x(n)$ for the system (2) at $b = 0.3$.

after $\mu > \mu_*$ for some $3 < \mu_* < 4$. In other words, the dispersion parameter $b$ will destabilize the system (2) when $0 < b < 1/2$ and $b$ is relatively large. For example, we take the initial data $x(-1) = 0.1$, $y(-1) = 0.2$, $x(0) = 0.3$, $y(0) = 0.1$; then by simulation we find that (i) the 2-periodic orbit loses stability and undergoes flip bifurcation when $\mu = 3.54$ and $b = 0.01$, $\mu = 3.51$ and $b = 0.03$, $\mu = 3.27$ and $b = 0.3$ respectively; (ii) $|x(n)| > 10$ for any $n \geq 30$ and $x(n) \to \infty$ for $n \geq 37$ when $b = 0.3$, $\mu = 3.6$; that is, the iterations are going outwards from the square $[0, 1] \times [0, 1]$ and evolving towards infinity.

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